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A NEW SPHENOPHYLLALEAN SHOOT SYSTEM FROM THE PENNSYLVANIAN

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INTRODUCTION

Investigations of American coal balls from the Pennsylvanian by Andrews and Mamay (1951), Baxter (1950), Hoskins and Cross (1943), and Mamay (1954; 1959) have greatly enlarged the anatomical knowledge of Sphenophyllalean fructifications; however, new petrified vegetative remains have not been described.

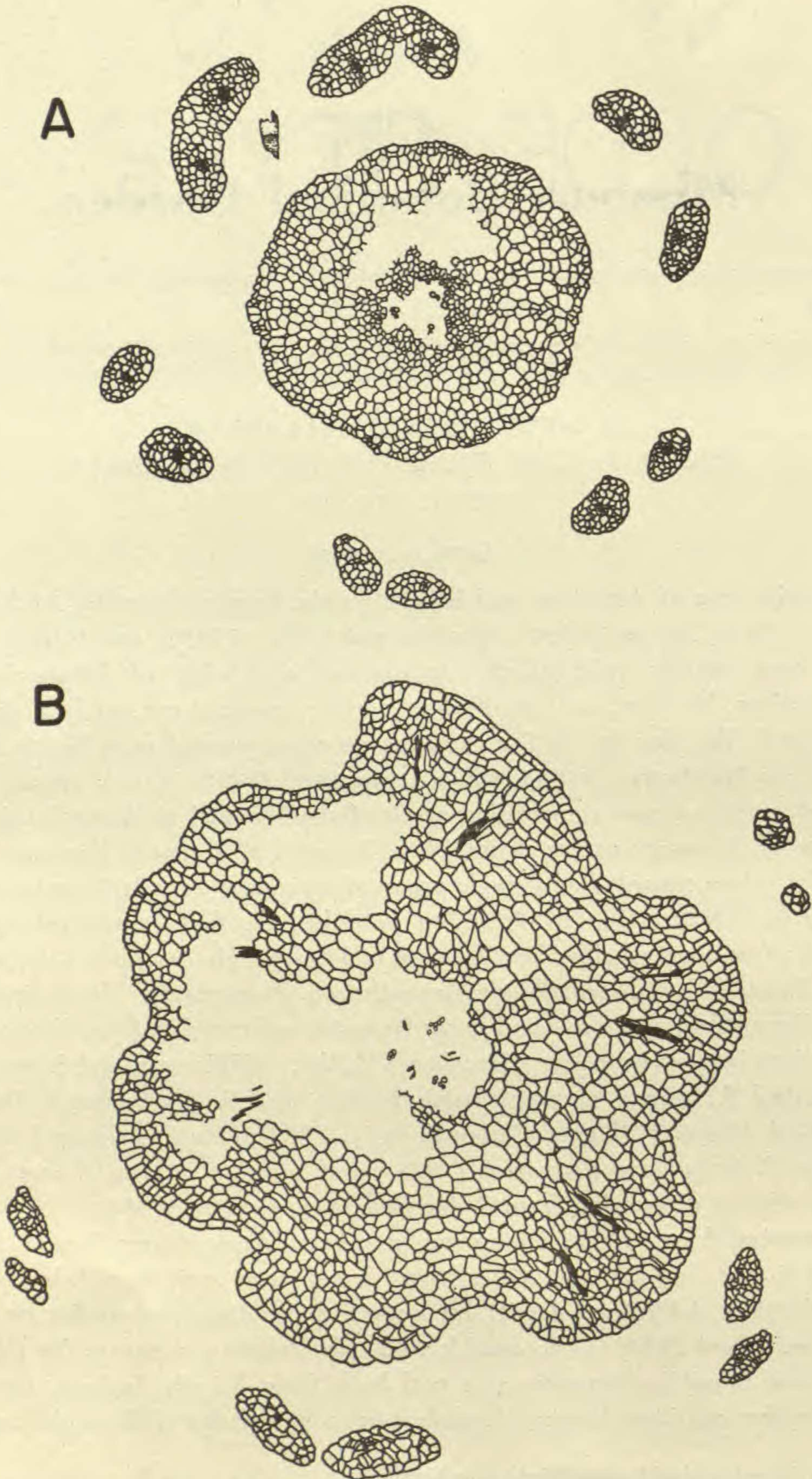
Sphenophylla referable to European species were reported from North America in Ohio by Newberry (1853) while Lesquereux (1858; 1860) among others, described numerous new compression species from Missouri to Pennsylvania. In a specimen of *S. emarginatum* from New Brunswick, Canada, Dawson (1865) found the xylem consisted of a single group of reticulate or scalariform vessels.

Renault (1870; 1873; 1876; 1878) published the first anatomical details of *Sphenophyllum* from silicified petrifications of France. He described *S. Stephanense* and *S. Renaultii* (*S. quadrifidum* Renault non Brongniart)¹ from Stephanian (upper-Upper Carboniferous) and lower Permian, and correlated petrifications with compressions in *S. cuneifolium* (Sternberg) Zeiller. Williamson and Scott (1894-5) described *S. insigne* (Lower Carboniferous) and *S. plurifoliatum* from the Lower Coal Measures (Upper Carboniferous). *S. Gilkineti* Leclercq (1925), *S. minus* and *S. perforatum* Koopmans (1928) were based on internodal anatomy and show insufficient distinction from *S. plurifoliatum*, (Baxter 1948).

Anatomical features thus far known have been largely drawn from *S. insigne*, *S. plurifoliatum*, and *S. Renaultii*; all were based upon some knowledge of node, leaf, and root. Additional details are known from American studies by Baxter (1948) and Reed (1949) who considered *S. plurifoliatum* adequate for the range of variation found in Pennsylvanian coal balls from Illinois, Indiana, Iowa, and Texas; further considerations are dependent upon knowledge of the nodal anatomy.

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¹ See Appendix.



Text Figure 1. *Sphenophyllum constrictum*, transverse sections.
A, Internode above (Slide 2743); B, Node (Slide 2739). $\times 20$.

MATERIALS

The following description was based upon nine plant fragments or groups of fragments.² Serial peels from such remains, with numerous other sections, were taken from three middle Pennsylvanian coal balls, two from Kansas and one from Indiana.

One was collected by Dr. Henry N. Andrews at a pit mine (Wasson Coal Mining Company) ten miles north of Booneville, Warrick County, Indiana. The coal is Petersburg or Alum Cave (Indiana No. 5 Coal) and correlative with Harrisburg (Illinois No. 5 Coal) of the Carbondale group, upper-middle Pennsylvanian. Two additional specimens were found by Dr. Sergius H. Mamay at a strip mine (Pittsburgh and Midway Coal Company) between West Mineral and Hallowell, Cherokee County, Kansas. The Fleming coal occurs in the upper part of the Cherokee shale, Des Moines series, middle-middle Pennsylvanian.

SPHENOPHYLLUM *constrictum* sp. nov.—General Description

Despite the generally parenchymatous nature of the plant, preservation is remarkably good. Various stages of development were preserved, which are referred to as young, mature, and old, although certainly they could represent portions of the same plant. The term young refers to portions displaying the primary body, often incomplete; mature, to secondary development without decortication; and old, to decorticated sections essentially of secondary tissue.

A comparative study of the plants from Kansas and Indiana was first initiated to determine their degree of similarity. Kansan material consisted of young and mature axes, and that of Indiana, mature to old. Mature stems in both provided bases for anatomical comparison. Figures 1 (Kansas) and 2 (Indiana) show the tissue relationships; anatomically, the two are not separable.

Nodal diameters of *S. constrictum* in mature stems are 4.5–5.0 mm. or about twice the internode of 2.5 mm.; the distance between nodes is 2.0 mm., resulting in a pronounced constricted appearance (fig. 4, 26). The shoot consists of a triarch exarch protostele with an adjoining parenchymatous cortex so characteristic as to easily separate *S. constrictum* from all other reported Sphenophylla. Dichotomizing leaf traces supply six bifid sessile leaves which are verticillate and superposed.

Text figure 1B shows the radially symmetrical nodal cross-section with six ridges intervened by grooves (one ridge is shown in fig. 14). The ridges are the six verticillate leaf bases which are distinct only as an equal number of leaves arise. The four pairs of leaf tips shown peripherally are from the node below; in young stems with slight internodal elongation, leaves exceed the height of the node next above. Diverging lines in leaf bases indicate passage of the dichotomized veins.

Text figure 1A shows the more rounded and reduced outline of the internode and the six whorled leaves which arose from the node of 1B, 0.45 mm. below.

² Roman numerals after each figure explanation indicate from which of the nine specimens the picture was taken.

The bifid nature of each leaf becomes apparent beyond one-half to two-thirds of the distinct leaf distance from the fluted node. The two distal portions are uninerved and tapered, with papillate to apiculate tips. The leaves usually curve slightly upward, markedly so in young stems, or may project straight out from the foliar disc (text fig. 2A).

STEM—PRIMARY TISSUE

The vascular zone of a young stem may lack central cells, depending on metaxylem maturation, but there are several tracheids ($15\text{--}20\ \mu$) preserved at deltoid vertices (compare text fig. 1B with fig. 14).³ In mature primary wood, merging of metaxylem cells ($20\text{--}55\ \mu$) with the three protoxylem groups is imperceptible except by the striking diminution of tracheid size toward each protoxylem vertex and the annular and spiral thickenings of the latter.

Metaxylem tracheids are best described as scalariform-reticulate. Although the thickenings are predominantly reticulate, there is transverse elongation toward the protoxylem (fig. 5). Elliptical to circular perforations of the radial and tangential walls appear to be simple pits, but previous reports (Renault 1878; Baxter 1948) indicate this is common due to border degradation. If the pits were bordered, the borders were quite fragile. Disintegration of protoxylary tissue resulting in lacunae occasionally occurred, but was local and discontinuous.

The area around the protostele is usually empty, and phloem is lacking. However, intervening tissue was preserved in the apical portion (fig. 22). Metaxylem is absent, and in the center are pyrite grains, not to be confused with the three equally black, in reality brown, groups of cells, CE, which alternate with the protoxylem; one group is preserved, PX. The three clusters of dark cells, CE, filled with resinous material, consists of 5–7 cells each, which are polygonal ($40 \times 90\ \mu$) in transverse section and serially appear to be connected in a linear manner. What such tissue represents is questionable, because no evidence was found that it contributes to the V-trace from the stele. Remnants of such cells are referable to the alternating vestiges of text figure 1B (CE, fig. 13–14).

Remains more comparable to nutrient conducting tissue, 2–3 cells thick, are radial to the protoxylem and peripherally delimited by a one cell layer (fig. 22). Such cells ($20\text{--}30\ \mu$), when separated by a V-trace, apparently join adjacent traces. Longitudinally, as in figure 10, cells with abutting transverse walls, PH, may represent phloem elements ($130\text{--}150\ \mu$ long).

The primary cortex which directly adjoins the stele without a distinct endodermis or pericycle, is highly characteristic and separates *S. constrictum* from all previously reported *Sphenophylla*. The entire cortex is parenchymatous with isodiametric polygonal cells up to $150\ \mu$; other species have thicker walled cortical tissue and occasionally remnants of an inner thin-walled cortex. The cortex accounts for four-fifths of the cauline diameter, and nodally there is no distinction

³ The term tracheid is used in all cases referring to xylary elements, but this in no way obviates the controversy of tracheid versus vessel (tracheae) in *Sphenophyllum*.

between this tissue and the leaf base. The cortical dimensions are extremely flexible due to secondary growth which resulted in internal compression and eventual decortication.

Parenchymatous tissue of the cortex and leaf is bounded by a layer of rectangular epidermal cells ($40 \times 80 \mu$ transversely), which often lack uniformity in shape and size. Epidermal cells are usually filled with brown to black residual matter, also seen in underlying cortical cells. In young plants, as in figures 26–30, cellular contents form a scattered pattern in the cortex, diminishing centripetally. In mature stems, most cortical cells are characterized by such residue, as in figures 1, 2, 9, and 10. In figure 7, a comparison in residual contents and relative development is shown between a main axis, A, and its branch.

STEM—SECONDARY TISSUE

Decorticated stems with abundant secondary wood present a problem of identification, but in several cases the distinct primary cortex was not completely obliterated (C, fig. 6).

Tracheids increase in size centrifugally in concentric and vertical rows, and those opposite primary xylary vertices often show little distinction from others. The number of concentric rows opposite sides of the triquetrous primary wood, however, need not be equal (fig. 12); this is common in *S. plurifoliatum*. Reticulate bordered pitting is more abundant on radial walls, and pits without borders resemble perforations of the metaxylem. Truncate tracheidal angles indicate un-preserved vertical parenchyma cells (PC, fig. 6).

Secondary phloem was absent, and there was always a gap between the wood and periderm. Periderm cells are $75\text{--}100 \mu$ long and often contain carbonaceous residue. The compact periderm gives way to a black amorphous tissue which clearly delimits the cortex.

LEAVES

Thin walled epidermis is covered by a scant cuticle, lacking in most cases; in direct contrast, *S. plurifoliatum* and *S. Renaultii* have a thickened epidermis. Stomata seems to be very scarce, but an opening suggestive of such, ST, from a transverse section of lower epidermis, is shown in figure 23. Cutinized structures on either side may represent guard cells, and behind is perhaps the slightly recurved margin of a guard cell. Other possible stomata have been reported by Renault (1876) in *S. Renaultii* and by Reed (1949) in *S. plurifoliatum*; openings were embraced by guard cells flush with the lower epidermis.

At nodes where branches were not observed, the pattern of leaf traces in the cortex is similar to other species, differing in relative position and number of ultimate veins. One V-trace originates from each protoxylem group. Six leaf traces horizontally tranverse the cortex to an equal number of fluted leaf bases. Actual connection of traces to the stele is not seen in mature plants with tissue lacking between wood and periderm, but distortions of the intervening tissues indicate the vascular passage (fig. 9). In stems with abundant secondary tissue, all

such evidence is lost. In the apical region, the V-trace was seen in connection with the protoxylem, which is clearly singular despite the twin trace emanation.

At the leaf base, the course of the trace descends slightly, gradually turns upward (LT, fig. 26) and then dichotomizes (B, fig. 10), supplying each leaf with a pair of veins. Text figure 1B (compare with fig. 14) shows a transverse section of leaf bases passing through the two veins indicated by heavy black lines; tips of four leaves from the node below are radial to the leaf bases. Figure 13, slightly oblique, shows partial separation of a leaf from the foliar disc and subsequent median constriction. Figure 15, from the apex, shows two superposed leaves almost divided. The ultimate tips of a leaf are seen in figure 8. The resulting verticillate phyllotaxy with leaves divided is shown in text figure 1A. The leaves appear elliptical to circular in cross-section and lack the more angular margins of other species.

Figure 11 (leaf enlargement from fig. 26, upper left) shows the undifferentiated mesophyll merging into the cortex without distinction. Epidermal and peripheral cortical cells characteristically have black-brown contents.

Vascular elements of the leaf consist of a concentric bundle of five to seven elements (V, fig. 8); tracheids are known from ringed and helical remnants. In a well preserved leaf section (LT, fig. 11) elongated thin walled elements with cross-walls are seen. Encircling the leaf supply is a one cell layer with brownish content (LT, figs. 28-29). The conducting system terminates near each bifid tip without further ramification.

BRANCHING

Branches were preserved in several developmental stages: primordial leaves (figs. 28-30), an elongated internode (fig. 31), and mature shoots (figs. 7, 32-33). They arise laterally in a variable association with leaves and are solitary at the nodes, but two are not uncommon. The branch trace originates at a vertex of the protostele, consequently, each branch is associated with one of three possible sets of leaves which derive their V-trace from the same vertex. When a branch arose, the V-trace of two associated leaves appeared to emanate with the branch trace, adjoining it below or laterally for a short distance.

Oblique cauline sections longitudinally through a nascent branch, as in figure 24 (enlargement of B, fig. 28), indicated the branch arose directly above a leaf by its relationship to the leaf trace, LT. Transverse serial sections of the young stem shown in text figure 1 presented two different branch-leaf relationships. In one case, a young branch apparently occupied the spatial position of the sixth leaf (text fig. 2A); the leaves extend straight out in the lower portion of this stem. Several peels later, the sixth and subtending leaf was seen in a mechanically displaced position similar to that in figure 29. Such growth between crowded superposed leaf whorls not only tends to push down the subtending leaf, but to displace the axis slightly. With subsequent growth, the branch slips toward one side of the leaf above. In a second case, two nodes lower, the branch arose almost exactly above and between two leaves. Such patterns were compared with other cases of branching; where the relationship of branch and leaf was ascertainable, branching

was as variable as the two extremes cited. Young branches as in figures 24, 28–31, and the above cases had no adventitious roots.

BASAL STEM

The unique axis of figure 19 was found adjacent to the stem of figures 26–27. The section was serially peeled on four faces, and with 1.9 mm. of matrix removed from each, the axis abruptly came to an end with the emanation of several roots. Organic connection of either end with other fragments was not established, but anatomical comparison and association leave little doubt of unity with *S. constrictum*. From the larger diameter and emanating roots, it is considered the lower portion of a shoot.

A perpendicular bisect of the triquetrous stele is about 0.9 mm.; cells range from 20–75 μ . The entire structure is 5.9 mm. in its largest dimension. The three cortical flares represent modifications of the foliar disc, below which a reduced rounded internode was seen.

Lacunose structures of the three cortical flares are characteristic of the entire stem portion, although some have been altered by degradation. Consequently, some peripheral lacunae of the cortex open to the exterior; others do not. The lack of foreign material in such cavities indicates they were originally closed and perhaps aerenchymatous in nature, though some may have possessed openings permitting the entrance of one to three spinose spherical bodies, 50 μ in diameter, which occurred in several chambers, but were not identified.

STEM APICES

The apex is shown longitudinally in figures 24 and 31, and obliquely transverse in figures 20 and 25. The cortical area of cell elongation is discernible (C, fig. 31), but vascular tissue is indistinct and completely obscure near the tip. In fig. 20, concentrically arranged cells indicate the proximity of the meristematic region, MR; fig. 25 is 0.7 mm. higher. Preservation above the stelar area was lacking, and the actual nature of apical division is speculative. Sections from apices indicate the newly formed cells are in a slightly domed series of uniform layers (fig. 24).

Spheroidal chambers, 70–120 μ in diameter, adjoining the adaxial leaf surface and frequently above a vein, were present in one apex (AC, figs. 20, 25) from the foliar disc to leaf bifurcation (AC, fig. 15). They result in slight to prominent bulges above the epidermis, but each cavity is apparently sealed by a layer of cuticle continuous with that of the epidermis (fig. 21). In no cases were they open to the exterior, even by degradation. Most chambers are devoid of contents; a few possessed small amounts of residue, and none exhibited internal structure.

Thin-walled cells delimit the remaining spheroidal space suggesting a structure of gaseous content. If air chambers, they may be analogous to a modified stomatal apparatus in which the stomatic cleft has permanently been roofed over with cuticle. Cavities are lacking or undiscernible elsewhere in the same and other stems, except in a few cases where they do not adjoin the epidermis, being separated by one to several cells (fig. 26, C). However, one lower stem fragment was characterized by lacunose areas.

ROOTS

Adventitious roots of *S. constrictum* are about 0.35 mm. in diameter, and their stelar size is denoted by the black endodermal ring (EN, fig. 17).

Delimitation of the root cortex from that of the stem is shown longitudinally in fig. 26. Figure 27 shows the root-stem vascular connection which is internodal even in such condensed articulations. Adventitious roots occurred singly or were abundant around branch bases. Branches up to the stage of development shown in figure 31 lack roots; this suggests the time sequence of root initiation. Roots emanated from branches in an adaxial to abaxial orientation, and remained singular or immediately bifurcated (figs. 32–33). Vascularization is near the main axis, but the root connection is with the branch and not at the node of the main axis. Adventitious roots were seen emanating from all parts of the stem except between leaves.

Larger roots were found attached to the axis in fig. 19. The root in fig. 16, 0.75 mm. in diameter, has two groups of uniformly small ($12\ \mu$) cells (5–6) near the center; from other sections the primary wood can not be described with certainty. Pitting of the secondary xylem is similar to that of the stem, but borders were not preserved (fig. 18). Periderm cells are $35\text{--}40\ \mu$ wide and compressed at their extremities merging with black amorphous tissue. Transversely, cells of the cortex are rectangular to polygonal and as large as $40 \times 100\ \mu$. Brown cellular contents typical of the cauline cortex are present.

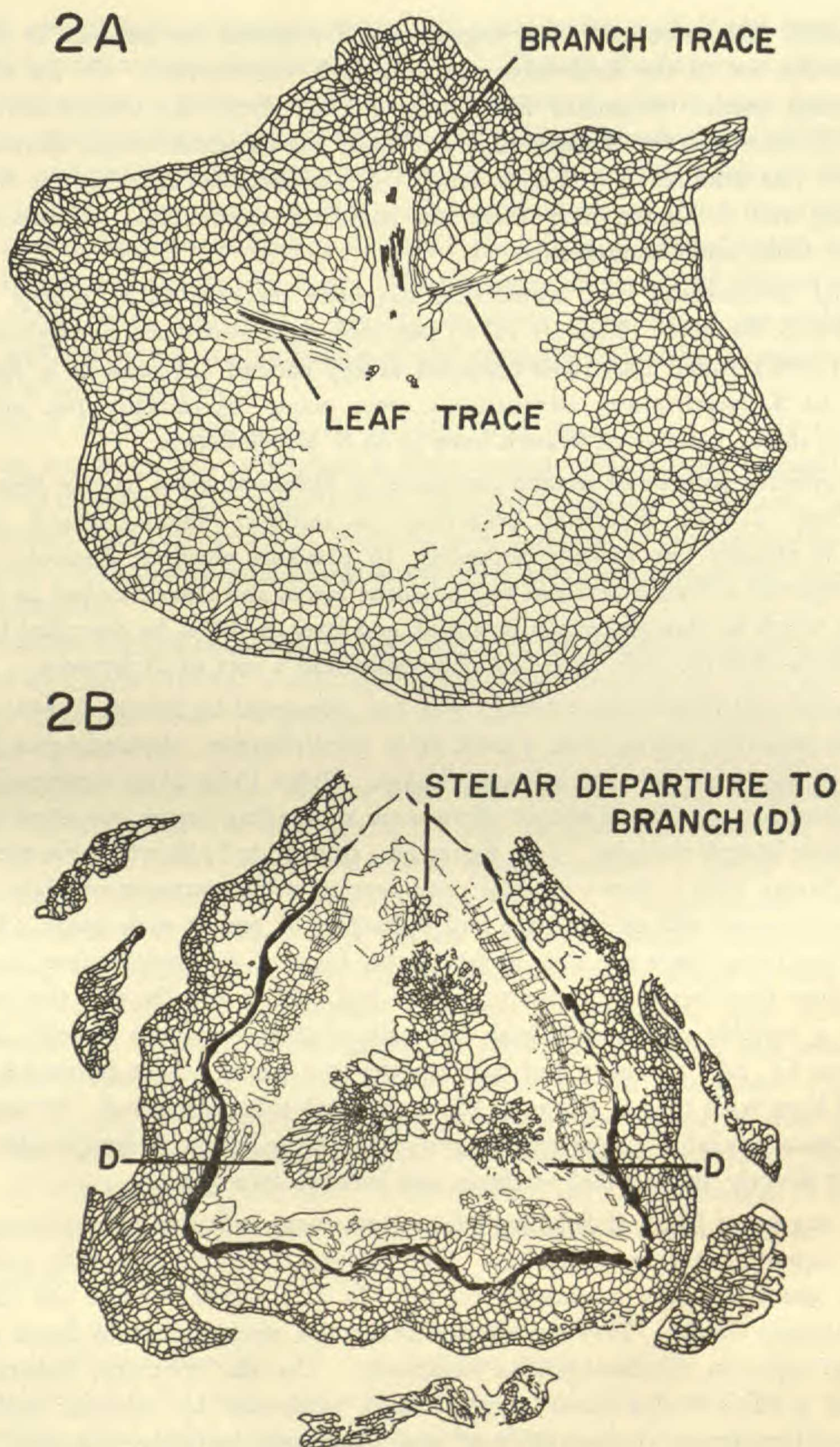
DISCUSSION

The cellular structure of the cortex and leaves of *S. constrictum* is quite distinct from that of other species; the cells are, throughout, uniformly thin-walled to a degree that suggests a plant of succulent habit. Although *S. Renaultii* and *S. plurifoliatum* have thin-walled inner cortical tissue, other differences between the two and *S. constrictum* are quite noticeable. Also, the ratio of cortical to xylary tissue in young stems is conspicuously greater than for other species.

The nodal diameter of *S. constrictum*, 4.5–5.0 mm., is comparable with those of *S. plurifoliatum* (4–6 mm.), *S. Renaultii* (3.6 mm.), and *S. Stephanense* (4.0–5.5 mm.). *S. Renaultii* is the only petrified species with a smaller internodal diameter (2.2 mm.) than *S. constrictum* (2.5 mm.). The nodes of *S. constrictum* are 2.0 mm. apart, markedly less than *S. Renaultii* (6–7 mm.) or *S. Stephanense* (10 mm.).

A perpendicular bisect of the primary wood in *S. constrictum* is 0.2–0.3 mm. compared to 0.4 mm. in *S. plurifoliatum* (Baxter 1948) and 1.0 mm. in *S. insigne* (Bower 1930). In addition to smaller size, the primary xylem in *S. constrictum* is very subject to degradation and crushing.

Sphenophyllum, in general, displays a distinctive leaf trace pattern, and *S. constrictum*, with three dichotomized V-traces, represents one of the simplest types. One or more traces may enter the leaf base in *Sphenophyllum*, with the number of terminal vein divisions usually coinciding with foliar segments or dentations (Renault 1882). Each leaf of *S. constrictum* has two ultimate veins



Text Figure 2. Nodal transverse sections with branch origins.
 2A, *Sphenophyllum constrictum* (Slide 2730); 2B, *S. plurifoliatum* (Slide 1539). $\times 17.5$.

and is bifid. Dichotomized foliar segments and venation are common in *Sphenophyllum* but not to the diminutive extent as in *S. constrictum*. Of the eighteen compression species recognized by Abbott (1958) from the United States and Canada, *S. fasciculatum* (Lesquereux) D. White has the most similar leaves in size and form (six bifid leaves 1–4 mm. long). *S. fasciculatum* also exhibits frequent branching and is known only from the middle-Pennsylvanian (Allegheny) of Missouri, Ohio, and Pennsylvania.

Nodal adventitious root connection has been reported in *S. insigne* (Scott 1920) and *S. Renaultii* (Renault 1878) but such attachment was not figured until Baxter (1948) found that roots occurred at any part of the stem in *S. plurifoliatum*. In *S. constrictum*, adventitious roots occur internodally but are most abundant in the vicinity of branch bases as in *S. plurifoliatum*.

The relative position of branch and leaves in *Sphenophyllum* has not been clear; Grand'Eury (1877) described branching as axillary; Solms-Laubach (1891) termed it obscure but axillary according to previous workers; Renault (1876; 1878) reported a branch between two adjacent leaves and also described an axillary swelling which he thought might be a bud, and later, in 1896, he described branching as extra-axillary, with some branches exhibiting a sort of dichotomy.

Detailed and illustrative evidence was first presented by Baxter (1948) showing three branches arising from a node of *S. plurifoliatum*. According to Baxter, branch origins were between adjacent leaves. Slides 1538–1542 representing the serial branching sequence indicate there were subtending leaves preserved at two of the three branch vertices. Text figure 2B (from slide 1539 referable to fig. 19, pl. 15, Baxter 1948) shows a nodal cross-section with remnants of eight leaves, two opposite each side of the stem and indicative of one at each angle. In such an interpretation, there are nine leaves in this form of *S. plurifoliatum*, and each of the three branches arose directly above a leaf. In *S. constrictum* the branches arose in a variable relationship with two associated leaves, from directly above a leaf (text fig. 2A) to above and between the two leaves. Text figure 2A shows five leaf bases with that of a branch above the sixth subtending leaf. In summary, the evidence available at present suggests that branches in *Sphenophyllum* may originate directly above a leaf or above and between two leaves.

The suggested habit of *Sphenophylla* ranges from suffrutescent herbs to lianas with an aquatic to terrestrial habitat. Hydrophytes have been repeatedly ruled out, and the genus has been considered ecologically as a whole because the anatomy was essentially similar. Previous species lacked the aerenchymatous tissue usually found in aquatics (Podostemaceae excepted). On the contrary, *Sphenophylla* exhibited a thick-walled outer cortex, leaves reinforced by sclerotic cells with substantial epidermal thickening, and well developed, extensive vascular tissue; all are indicative of a plant adapted to land (Reed 1949). Size and habit from compression forms, some with dorsi-ventral verticils, further substantiated a scrambling or climbing liana.

In *S. constrictum*, epidermal and cortical tissue is thin-walled, and development of wood is more meager than in other species. Though the nature of chambers in the apical portion is dubious, the cortical structure of a lower stem fragment is lacunose. Such evidence infers a semi-aquatic habitat. Lack of mesophyll differentiation and limited cuticular development conform with such an inference (Arber 1920). The abundant thin walled cortical tissue, short internodes, and forked needle-like leaves suggest a succulent plant, though the epidermal walls are relatively thin and the cuticle scant. The character of peripheral cellular contents of the plant would also have a bearing on water retention or loss (Maksimov 1929), but the nature or significance of the characteristic cellular residue in stem and leaf is only conjectural.

Stems of described *Sphenophylla* probably were aerial, but it is likely that basal anchoring was frequently submerged in their swampy environment (Arnold 1947). Divergence in habitat of *S. constrictum*, indicated by anatomy and habit, from the contemporary coal ball species, *S. plurifoliatum*, may not be as drastic then as first envisioned. Both species were found in the same coal balls, though the former was better preserved.

Rhizonium verticillatum Williamson (1889), of the heterogeneous root genus established by Corda (1845), is strikingly similar to *S. constrictum*. An examination of slides 1234 and 1909 (Williamson Collection) confirms Williamson's descriptions and figures (162-3, figs. 16-21, 1889); however, the axes are those of stems with verticillate leaves rather than of roots with rootlets. Seven nodes are shown in longitudinal section, 1.6 mm. apart, 1.5 mm. in nodal diameter, and 1.2 mm. internodally. The metaxylem of the triarch exarch protostele is clearly scalariform and distinctly different from that of *S. constrictum*. A perpendicular bisect of the xylem is 0.14-0.18 mm.; there are no secondary tissues. Indistinct tissue surrounding the xylem adjoins the parenchymatous cortex which is thin-walled, the outermost cells (2-3) slightly thicker, homogeneous, and continuous with that of the leaves; this was apparently succulent in nature and remarkably like that of *S. constrictum*. Amber colored cellular residue is lacking. The leaves are about 1.5 mm. in length, but the actual number and nature of their tips can not be determined from the thin sections. *R. verticillatum* apparently represents a form of *Sphenophyllum* previously overlooked in the Coal-Measures of England and is quite similar to *S. constrictum* from American coal fields.

SPHENOPHYLLUM constrictum Phillips, sp. nov.

Diagnosis: Articulated stem, 4.5-5.0 mm. nodal diameter (less than 6.0 mm.), 2.5 mm. internodal diameter, 2.0 mm. between nodes; exarch, triarch protostele, primary bisect 0.2-0.3 mm., metaxylem pitting scalariform-reticulate; tracheids of secondary wood radial to protoxylem often show little distinction from others in size, pitting bordered-reticulate; compact internal periderm bordered by black amorphous tissue; cortex and epidermis of thin parenchymatous tissue with dark residual contents, cortex of lower stem lacunose, air chambers scant elsewhere; cuticle thin or absent.

Leaves six in each verticil, not over 1.5 mm. long, bases fused and bifid in distal portion, circular to ellipsoidal in cross-section, cellular structure continuous with that of cortex, probably succulent in life; vascular supply initiates as 3 V-traces which divide in cortex to 12 with one strand entering each bifid segment.

Lateral branches originate above leaf or above and between leaves.

Adventitious roots, 0.35–0.75 mm. diameter, primary xylem not determined, rectangular to polygonal cortical cells with characteristic cauline contents, secondary tissue similar to stem, attachment internodal to vicinity of node.

Holotype: Slides 2641–2790 from WCB# 1026, paleobotanical collections of The Henry Shaw School of Botany, Washington University.

Locality: Hallowell-West Mineral, Cherokee County, Kansas

Horizon: Fleming, Des Moines Series, middle-Pennsylvanian

Paratypes: Slides 2791–2829 and WCB# 921-2-3A-3B

Locality: North of Booneville, Warrick County, Indiana

Horizon: Petersburg V, middle-Pennsylvanian

Paratypes: Slides 2830–2910 and WCB# 1025 D-E-F

Locality and Horizon of Holotype.

SUMMARY

Developmental stages, including lower stem and apical portions, of a new vegetative shoot system, *Sphenophyllum constrictum*, were described from the middle-Pennsylvanian of Indiana and Kansas. Branch origins were found to be directly above to above and between leaves and adventitious roots emanated internodally to nodally, more frequently at branch bases. The following features of *Sphenophyllum* were exhibited by the new species.

1. Exarch triarch protostele.
2. Six sessile superposed verticillate leaves supplied with dichotomized V-traces.
3. Compact periderm and secondary xylem with intercellular spaces at truncate tracheidal margins and reticulate bordered pitting.

The following different characters easily distinguish *S. constrictum*:

1. Epidermal and cortical tissue consists of thin-walled cells with dark residual contents; lower stem with lacunose cortex. The cortex of stems without secondary growth constitutes as much as four-fifths of the diameter.
2. The leaf supplies are derived from three dichotomized V-traces which give rise to twelve veins, two per leaf, one for each bifid segment.
3. The six bifid leaves are 1.5 mm. or less in length from a foliar disc 4.5–5.0 mm. in diameter, with internodal diameter of 2.5 mm. and 2.0 mm. between nodes; the constricted outline is evident in all but transverse sections and decorticated material.

ACKNOWLEDGMENTS

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APPENDIX

Renault referred to *S. quadrifidum* Renault (non Brongniart) both as a species and subspecies, (*S. angustifolium* (Germar) Goeppert subsp. *quadrifidum* Renault), although the latter never appeared as a combination. A new specific epithet is proposed with the below listed type description citation and subsequent illustrative references:

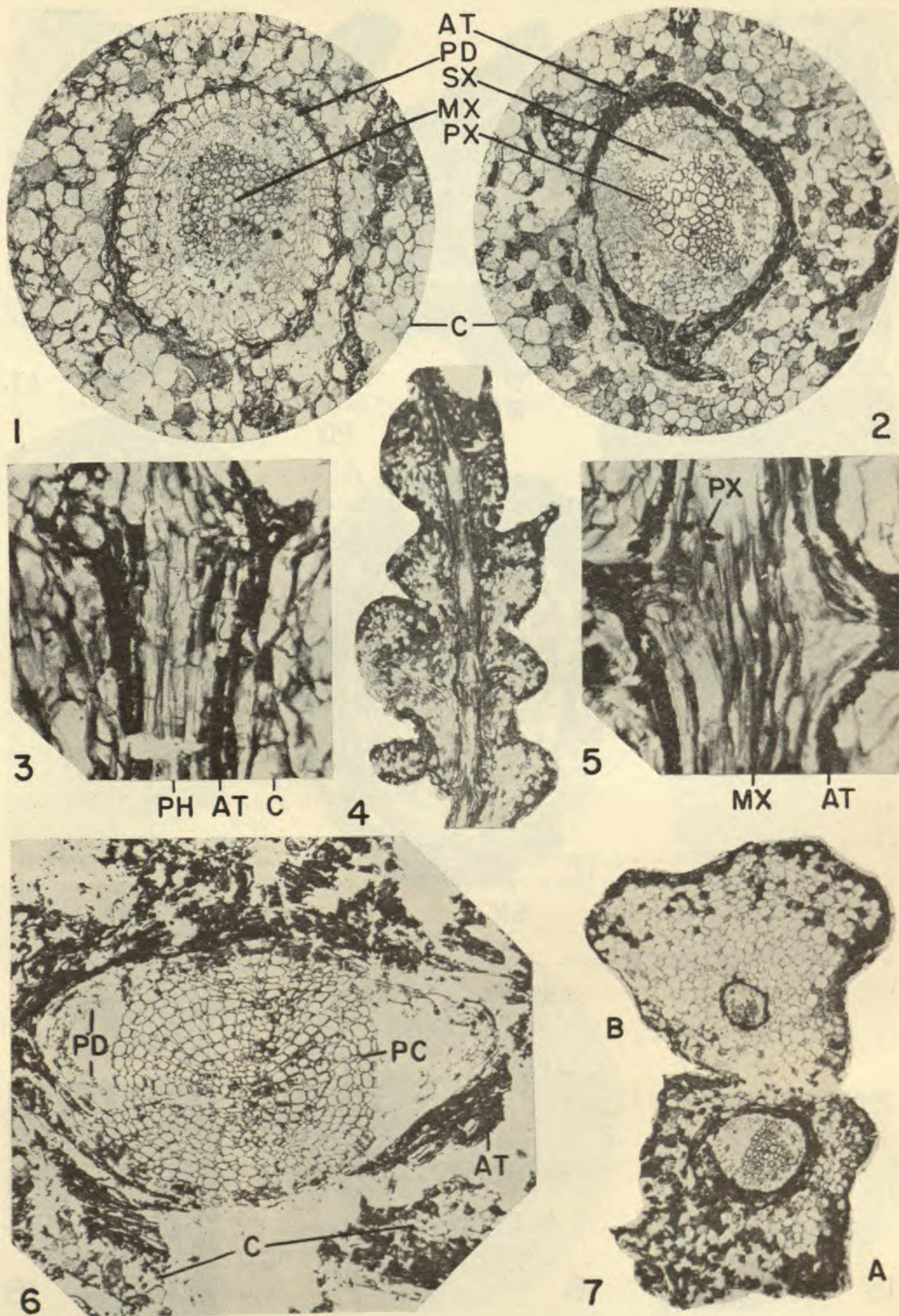
SPHENOPHYLLUM *Renaultii* Phillips nom. nov.

- 1876 *Sphenophyllum quadrifidum* B. Ren., Végétaux Silicifiés d'Autun et de Saint-Étienne, Nouvelles Recherches sur la Structure des Sphenophyllum et sur Leurs Affinités Botaniques, Annals des Sciences Naturelles, sér. 6, Botaniques, 4:293-299, pl. 7, figs. 1-3, non Brongniart, 1828, Prodrome d'une Histoire des Végétaux Fossiles, p., 76 (68).
- 1878 *S. quadrifidum* in Renault, Recherches sur la Structure et les Affinités Botaniques des Végétaux Silicifiés, Autun, 178-183, pl. 28, figs. 1-2.
- 1880 *S. quadrifidum* in Schimper, in Zittel, Handb. Paläont., 177, Fig. 134, 1-3.
- 1882 *S. quadrifidum* in Renault, Cours de Botanique Fossile, 2:89, 93-97, pl. 15, figs. 1-3.
- 1887 *S. quadrifidum* in Solms-Laubach, Einl. Paläophyt., 356, Fig. 48, 1-3.
- 1891 *S. quadrifidum* in Solms-Laubach, Fossil Botany, Oxford, 347, text fig. 48, 1-3.
- 1900 *S. quadrifidum* in Scott, Studies Foss. Bot., 83, text fig. 34; 2d ed., 1908, 1:80, text fig. 36; 3d ed., 1920, 1:79, text fig. 38.
- 1927 *S. quadrifidum* in Hirmer, Handb. Paläobotanik, 351, 353, Fig. 410.
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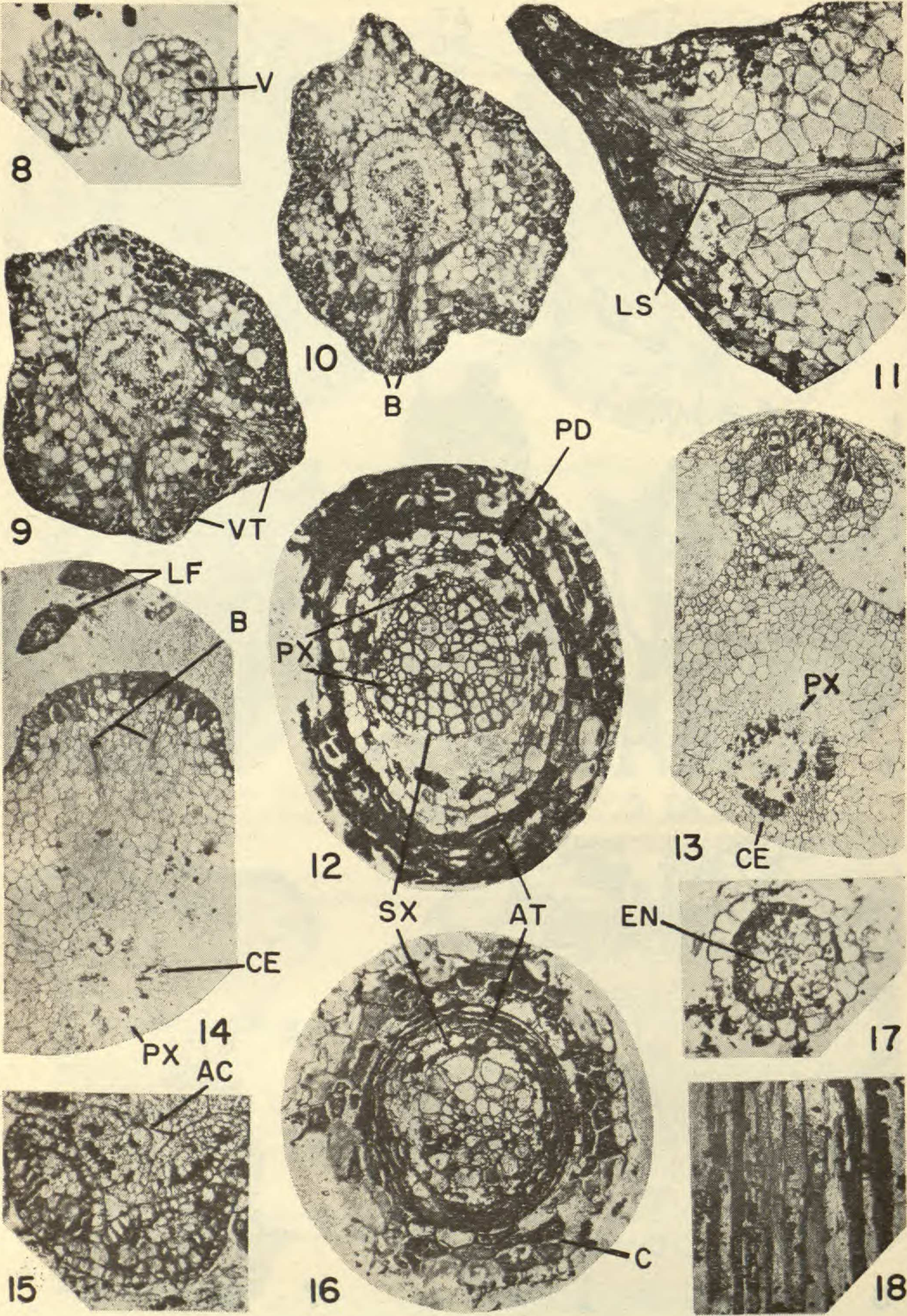
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Figure 1.	Transverse section of mature stem from Kansas. MX, metaxylem; PD, periderm; C, cortex.	
	Slide 2856	IX
		× 35
Figure 2.	Transverse section of mature stem from Indiana. PX, protoxylem; SX, secondary xylem; AT, amorphous black tissue between periderm and C, cortex.	
	Slide 2800	VII
		× 35
Figure 3.	Enlarged longitudinal section of mature stem shown in fig. 4. PH, possible phloem; AT, amorphous black tissue; C, primary cortex.	
	Slide 2797	VI
		× 58
Figure 4.	Longitudinal section of mature stem showing four nodes, from Indiana.	
	Slide 2797	VI
		× 7
Figure 5.	Enlarged longitudinal section of mature stem shown in fig. 4. PX, protoxylem; MX, metaxylem; AT, amorphous black tissue.	
	Slide 2797	VI
		× 58
Figure 6.	Transverse section of stem. PC, spaces at the truncate margins of secondary xylem indicating unpreserved parenchyma; PD, periderm; AT, amorphous black tissue; C, vestiges of sloughed off cortex.	
	Slide 2796	VI
		× 22
Figure 7.	Oblique transverse section of main axis, A, and branch, B. Note the residual cellular content pattern and the stelar development.	
	Slide 2805	VII
		× 9



PHILLIPS—SPHENOPHYLLUM CONSTRICTUM



PHILLIPS—SPHENOPHYLLUM CONSTRICTUM

EXPLANATION OF PLATE

PLATE 2

Sphenophyllum constrictum sp. nov.

- Figure 8. Transverse section of the two tips of a leaf taken from the apex. V, vein.
Slide 2723 $\times 112$ I
- Figure 9. Transverse section of mature stem. VT, V-trace or twin traces passing through the periderm, black amorphous tissue, and cortex.
Slide 2856 $\times 18$ IX
- Figure 10. Serial peel sequence of figure 9; B, one leaf trace of V-trace divided into two veins.
Slide 2856 $\times 18$ IX
- Figure 11. Enlarged longitudinal section of leaf of figure 26, upper left. LT, elongated conducting elements. Note undifferentiated mesophyll of leaf and leaf base.
Slide 2761 $\times 35$ III
- Figure 12. Transverse section of a decorticated branch. PX, protoxylem; PD, periderm; AT, black amorphous tissue, SX, secondary xylem. Note unequal development of secondary xylem.
Slide 2799 $\times 63$ VII
- Figure 13. Sector of oblique transverse section from young stem showing a leaf almost separated from the foliar disc. PX, protoxylem; CE, tissue referable to that in figs. 14, 22.
Slide 2708 $\times 35$ I
- Figure 14. Sector of transverse section from young stem. LF, two tips of a leaf from node below; B, two veins cut tangentially in leaf base; CE, tissue of uncertain nature which alternates with the protoxylem, PX.
Slide 2739 $\times 35$ II
- Figure 15. Oblique transverse section from apex. Two superposed bifurcating leaves from successive nodes. AC, chamber bulging out on upper epidermal leaf surface.
Slide 2717 $\times 63$ I
- Figure 16. Transverse section of mature root. SX, secondary wood; AT, amorphous black tissue; C, cortex.
Slide 2762 $\times 63$ IV
- Figure 17. Transverse section of young adventitious root. EN, endodermal ring.
Slide 2879 $\times 58$ VIII
- Figure 18. Oblique longitudinal section of mature root showing reticulate pitting of the secondary xylem.
Slide 2760 $\times 63$ IV